

# Sistemas reproductivos

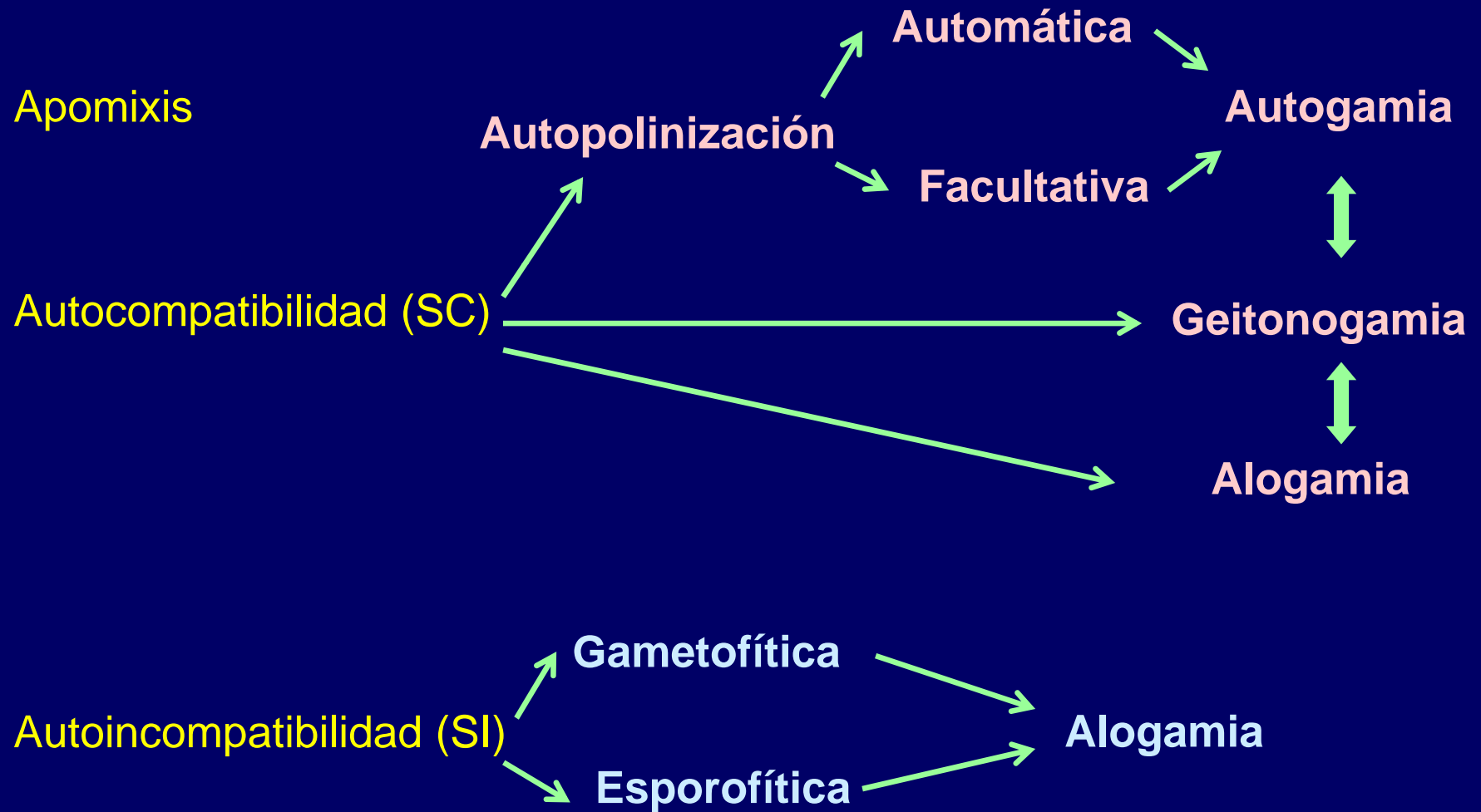


TABLE 2. Plant species, growth forms (H = herb, S = shrub, T = tree, E = epiphyte, Hp = hemiparasite), principal visitor categories observed, and results of controlled pollinations. Other sources on compatibility are cited when available. SI = self-incompatible, SC = self-compatible. A question mark indicates an "educated guess," i.e., the absence of conclusive evidence on breeding system. Hand-pollinations in three of the four *Acacia* species were unsuccessful.

Species	Growth form	Visitor type	(n)‡	Fruit set* (n)†				Com- pati- bility
				Emascu- lated	Control	Self- pollinated	Cross- pollinated	
Acanthaceae								
<i>Justicia squarrosa</i> Griseb.	H	Butterflies	10	0 (20)	0 (30)	0.25 (40)	0.35 (34)	SC
Bromeliaceae								
<i>Tillandsia lxioides</i> Griseb.	E	Hummingbirds	16	0 (20)	0 (25)	0 (25)	0.85 (26)	SI
Cactaceae								
<i>Opuntia quimilo</i> R. Schum.	T	Medium-sized to large bees	3	...	0 (5)	0 (5)	0.50 (6)	SI ?
<i>Rhipsalis lumbricoides</i> Lem.	E	Butterflies, bees, wasps	6	0 (55)	0.05 (60)	0.10 (60)	0.78 (60)	SI
Capparaceae								
<i>Atamisquea emarginata</i> Miers	S	Bees  , wasps, moths	3	...	0 (180)	0.02 (130)	0.47 (130)	SI
Leguminosae: Caesalpinoideae								
<i>Caesalpinia gilliesi</i> Wall. ex Hook.	S	Hawk moths	6	...	0.03 (226)	0.23 (47)	0.35 (40)	SC
<i>Cassia aphylla</i> Cav.	S	Large bees	3	...	0 (35)	0.45 (29)	0.28 (32)	SC§
<i>Cercidium australe</i> Johnst.	T	Bees  , wasps	5	...	0 (500)	0.01 (166)	0.32 (177)	SI§
Leguminosae: Mimosoideae								
<i>Acacia aroma</i> Gill.	S, T	Medium-sized to large bees	3	...	... (94)	... (46)	... (45)	SI§
<i>A. atamentaria</i> Benth.	T	Bees, beetles	4	...	... (40)	... (24)	... (25)	SI ?
<i>A. furcatispina</i> Burkart	S	Butterflies, bees, wasps	4	...	... (264)	... (107)	... (152)	SI§
<i>A. praecox</i> Griseb.	S, T	Bees  , wasps	6	...	0 (250)	0.05 (83)	0.21 (99)	SI
<i>Mimosa detinens</i> Benth.	S	Moths, wasps	5	...	0.05 (150)	0.45 (162)	0.81 (164)	SC
<i>Prosopis nigra</i> (Griseb.) Hieron.	T	Bees  , flies, wasps	5	...	0 (24)	0 (19)	0.85 (19)	SI§
Loranthaceae								
<i>Ligaria cuneifolia</i> (R. et P.) Tieghem	Hp	Hummingbirds	6	0 (97)	0.10 (107)	0.26 (79)	0.34 (67)	SC
Portulacaceae								
<i>Portulaca umbraticola</i> H.B.K.	H	Small bees, butterflies	18	0.10 (10)	0.61 (23)	1.00 (26)	1.00 (32)	SC

\* Number of fruits/flower (or per inflorescence in the Mimosoideae).

† Number of flowers (or inflorescences in the Mimosoideae).

‡ Number of plants.

§ Information on incompatibility also reported in Neff et al. (1977).

|| Including a large proportion of visits by honey bees (*Apis mellifera*).

Aizen M.A. y P. Feinsinger. 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75: 330-351.

TABLE 1. Frequency of self-incompatibility and dioecy (obligate outcrossing, SI + D) in different plant communities. Studies are considered to be tropical if they were performed between the tropics of Cancer and Capricorn, temperate if not. Of the Island studies, only that of McMullen is tropical by this criterion. Habitat: woody, only woody plants examined; herb, only herbaceous; mixed, both growth forms examined.

Flora	n	SI + D	Habitat	Study
<b>Mainland</b>				
Temperate				
Canadian forest herbs	12	41.7%	herb	Barrett and Helenurm 1987
Canadian salt marsh	17	29.4%	herb	Pojar 1974
Canadian bog	28	32.1%	herb	Pojar 1974
Canadian subalpine meadow	37	48.6%	herb	Pojar 1974
New England shrubs	12	41.7%	woody	Rathcke 1988
North Carolina forest wildflowers	11	27.3%	herb	Motten 1986
U.S. and Argentine deserts	26 <sup>a</sup>	76.9%	woody	Neff et al. 1977
Patagonian alpine flora	124 <sup>b</sup>	34.1%	herb <sup>a</sup>	Arroyo and Squeo 1990
Chilean temperate dry forest	37 <sup>b</sup>	43.5%	mixed	Arroyo and Uslar 1993
Chilean valdivian forest	39 <sup>b</sup>	46.4%	mixed	Riveros et al. 1996
Argentine chaco forest	15 <sup>a</sup>	60.0%	mixed	Aizen and Feinsinger 1994
Argentine chaco forest	32 <sup>a</sup>	43.8%	mixed	Morales and Galetto 2003
Argentine chaco understory	7 <sup>a</sup>	85.7%	woody	Bianchi et al. 2000
Tropical				
Mexican deciduous forest	33 <sup>b</sup>	79.1%	woody	Bullock 1985
Costa Rican dry forest	34 <sup>b</sup>	84.0%	woody	Bawa 1974
Costa Rican Lowland Forest	64 <sup>b</sup>	61.3%	mixed	Kress and Beach 1994
Brazilian savanna, near Brasilia	30 <sup>b</sup>	81.0%	woody	Oliveira and Gibbs 2000
Venezuelan tropical dry forest	49 <sup>b</sup>	55.2%	mixed	Jalms and Ramirez 1999
Venezuelan palm swamp	25 <sup>b</sup>	22.5%	mixed	Ramirez and Brito 1990
Venezuelan cloud forest	25 <sup>b</sup>	53.0%	mixed	Sobrevilla and Arroyo 1982
<b>Islands</b>				
Chiloe Island, Chile	20	60.0%	woody <sup>a</sup>	Smith-Ramirez et al. 2005
Galapagos Islands, Ecuador	51 <sup>b,c</sup>	5.0%	mixed	McMullen 1990
Juan Fernandez Islands, Chile	22	40.9%	mixed	Anderson et al. 2001
Montane rainforest, Jamaica	8 <sup>b</sup>	30.9%	woody	Tanner 1982
New Zealand	47 <sup>b,d</sup>	32.7%	mixed	Newstrom and Robertson 2005
<b>Total:</b>	<b>805</b>	<b>48.7%</b>		

<sup>a</sup> These studies did not estimate the proportion of the flora that is dioecious.

<sup>b</sup> Sample size listed is only for tests of self-compatibility in hermaphrodites. Dioecy was estimated separately from a larger dataset.

<sup>c</sup> The estimate for dioecy is from Baker and Cox (1984).

<sup>d</sup> The estimate for dioecy is from Carlquist (1966).

<sup>e</sup> One or two species in sample have the alternative growth form.

Igic, B. y J.R. Kohn. 2006. The distribution of plant mating systems: study bias against obligately outcrossing species. *Evolution* 60: 1098–1103.

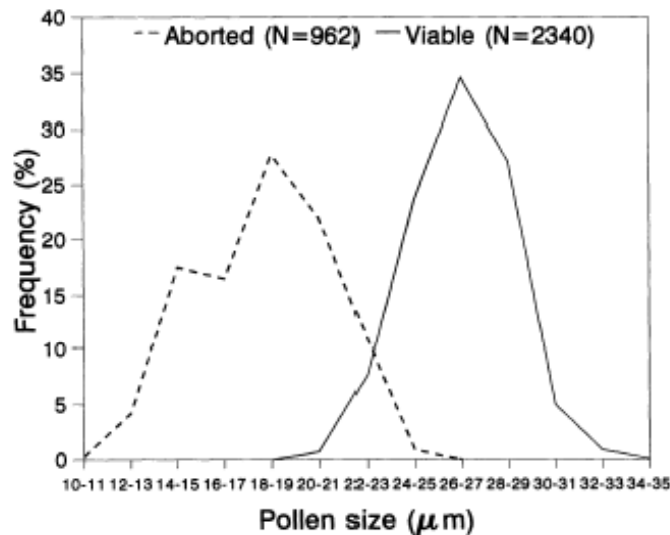


Fig. 1 Frequency distributions of pollen diameter of aborted and nonaborted pollen grains of *Austrocedrus chilensis*

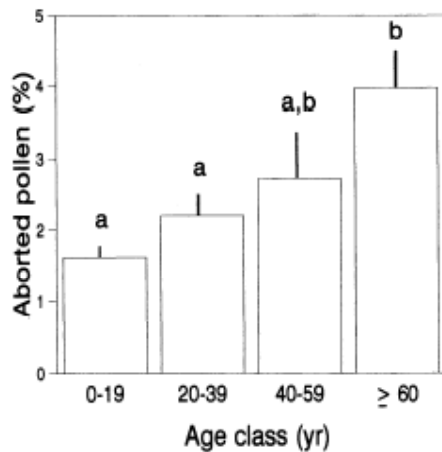


Fig. 3 Mean proportion (+SE) of aborted pollen grains for each of 20-yr age intervals. Means that share the same letter do not differ significantly at  $P < .05$  (Tukey's test). Sample sizes are: 40, 25, 7, and 6 trees for the 0-19, 20-39, 40-59,  $\geq 60$  yr classes, respectively.

Aizen, M.A. y A.E. Rovere. 1995. Does pollen viability decrease with aging? A cross-population examination in *Austrocedrus chilensis*. International Journal of Plant Sciences 156: 227-231.

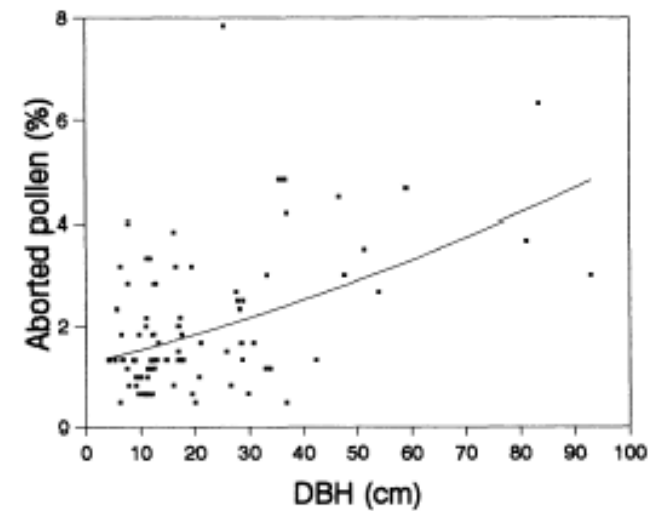
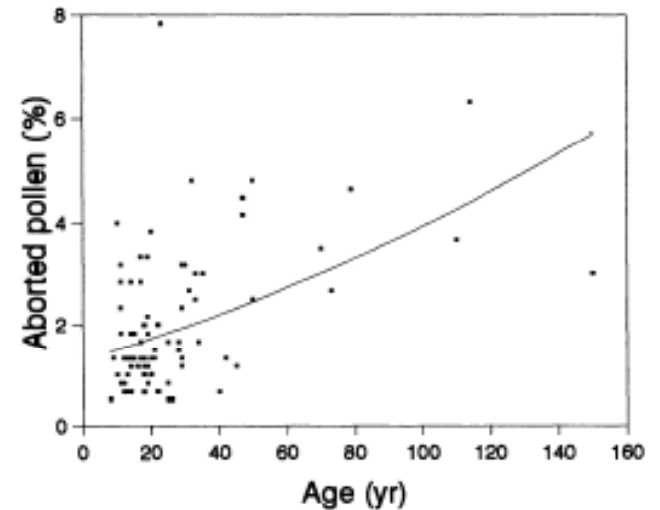


Fig. 2 Proportion of aborted pollen versus tree age and versus tree diameter at breast height. Back transformed least-square regression lines are depicted. Regression equations are  $Y' = .1147 + .00085 X$ ,  $Y = .1124 + .0012 X'$ ; where  $X$  and  $X'$  are tree age and DBH, respectively,  $Y$  is the arcsin (square-root) transformation of the proportion of aborted pollen.



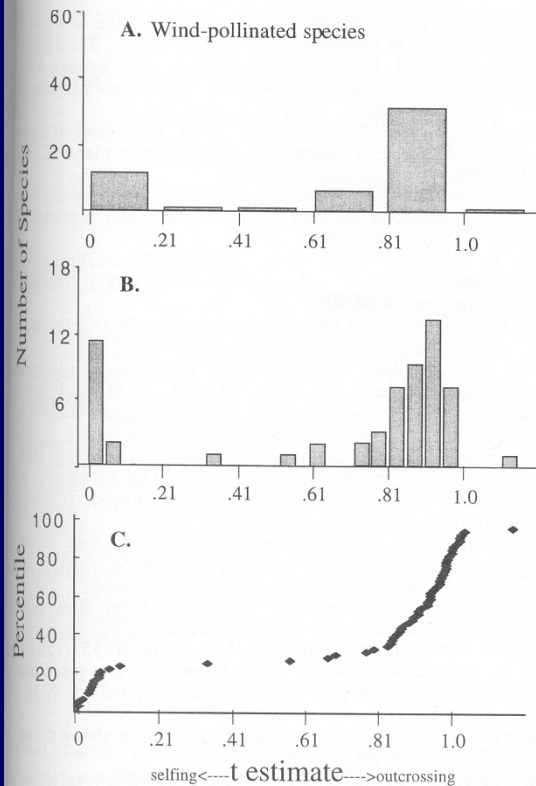


FIG. 1. Distribution of  $t$  estimates for  $n = 59$  wind-pollinated plant species presented in three graphical forms. (A) Frequency histogram with data classes of 0.20 intervals. (B) Frequency histogram with data classes of 0.05 intervals. (C) Plot of percentile vs. ranked  $t$  estimate data.

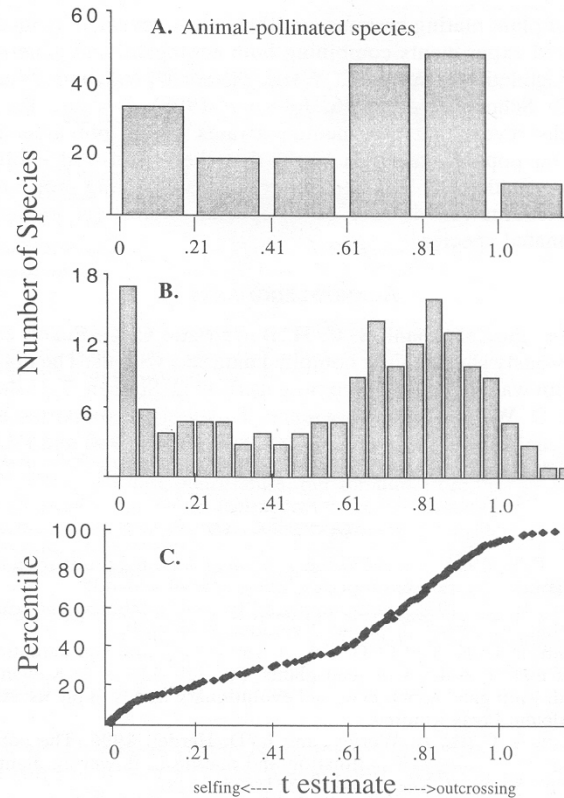
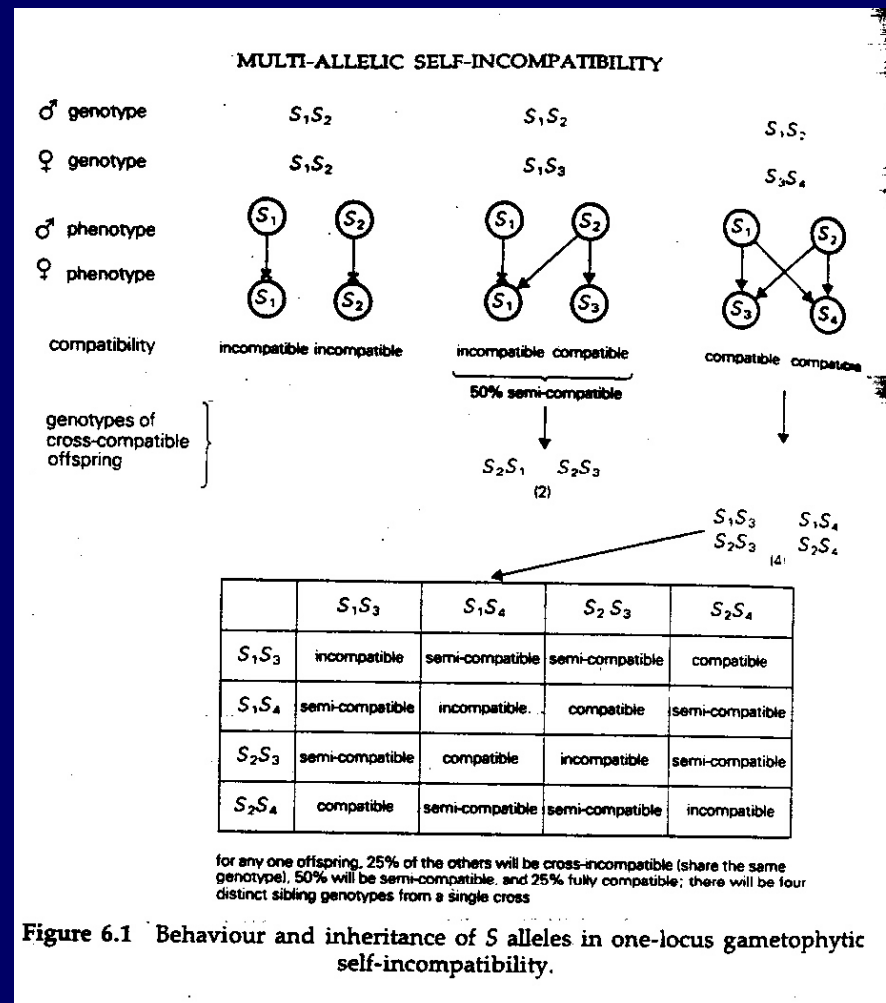


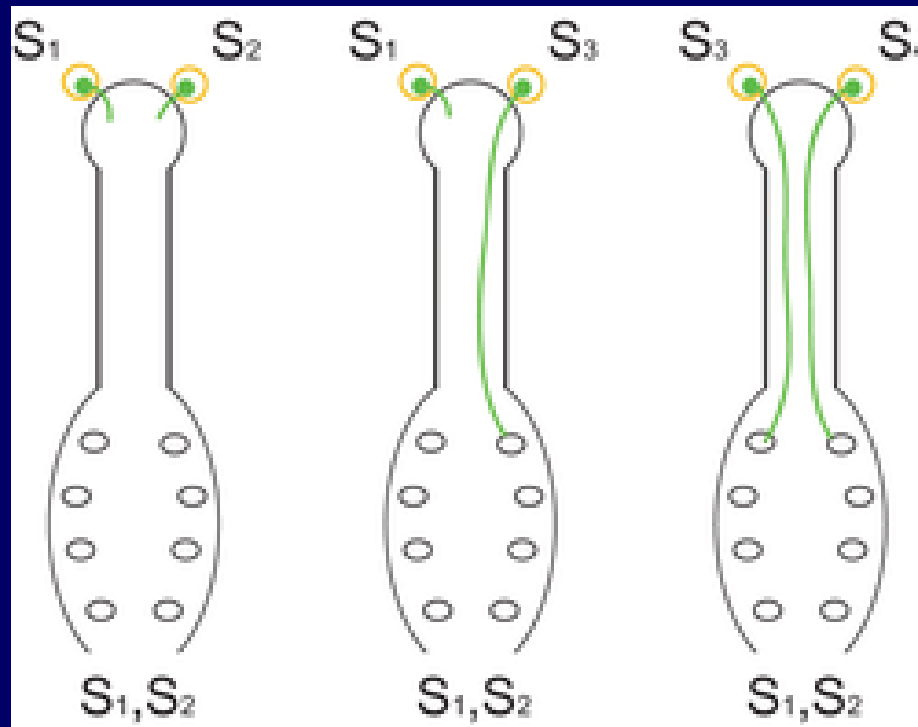
FIG. 2. Distribution of  $t$  estimates for  $n = 169$  animal-pollinated plant species presented in three graphical forms. (A) Frequency histogram with data classes of 0.20 intervals. (B) Frequency histogram with data classes of 0.05 intervals. (C) Plot of percentile versus ranked  $t$ -estimate data.

Vogler, D.W. y S. Kalisz. 2001. Sex among the flowers: the distribution of plant mating systems. *Evolution* 35: 202-204.

# Autoincompatibilidad



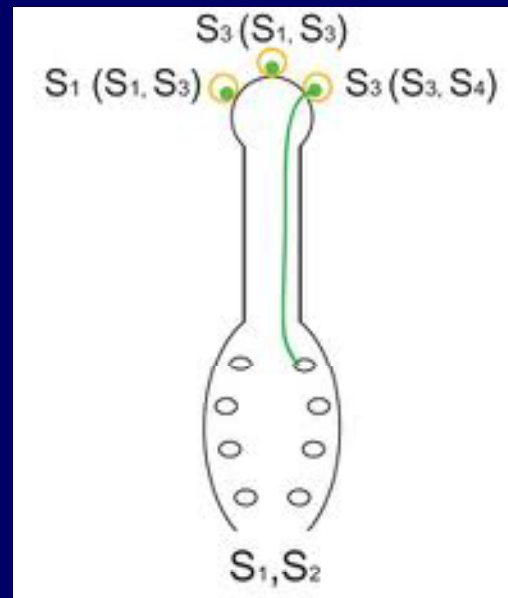
## Autoincompatibilidad gametofítica



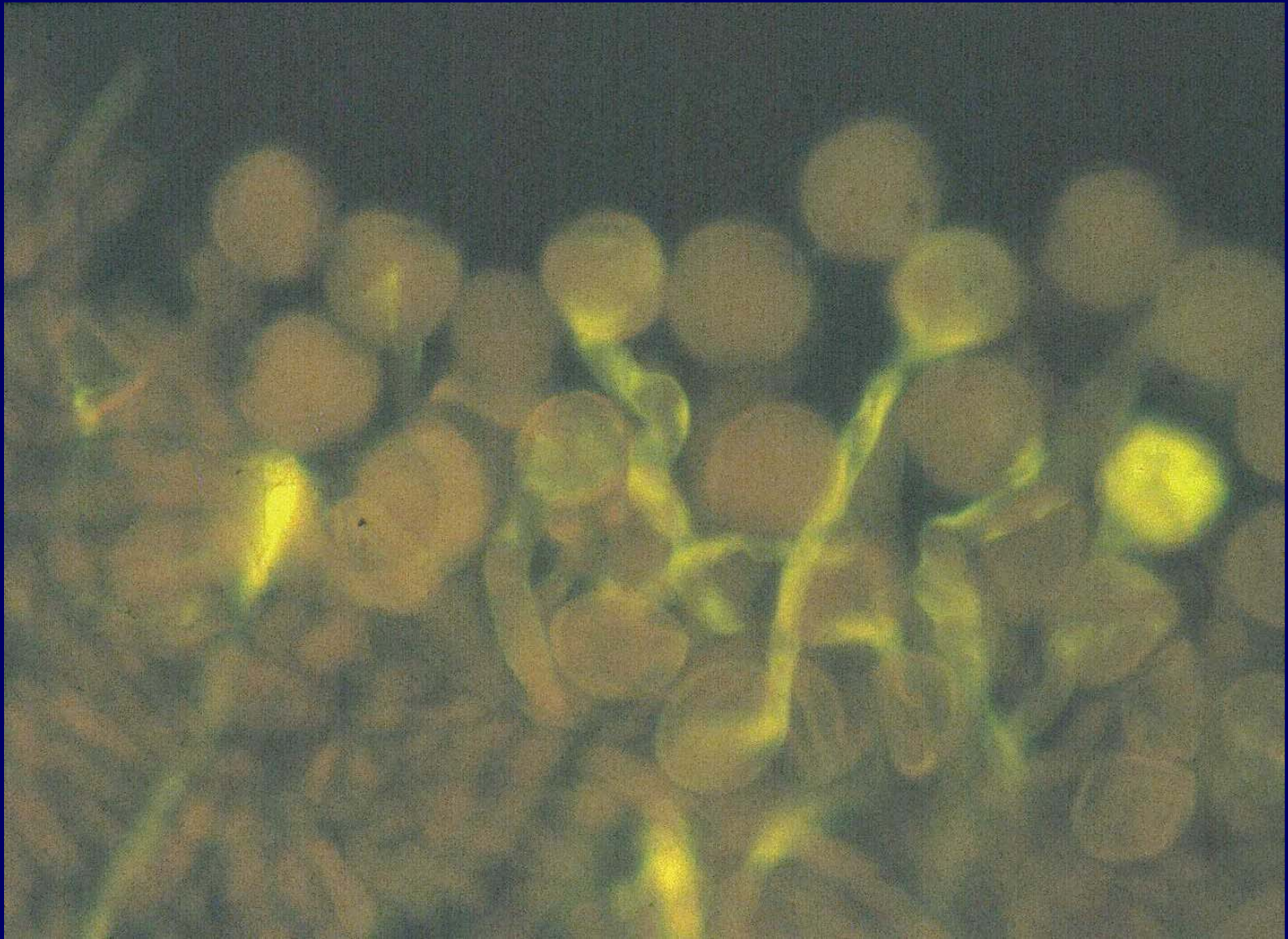




## Autoincompatibilidad esporofítica







## Dicogamia (protandria y protoginia)







Fig. 1. Sequential diagrams representing the sexual life stages of a typical *A. aurea* flower (lateral view). Stage 0, flower just right after anthesis, no dehiscent anthers; stage I, young male phase, flowers with one or two dehiscent anthers; stage II, intermediate male phase, flowers with three or four dehiscent anthers; stage III, advanced male phase, flowers with five or six dehiscent anthers; stage IV, neuter phase, anthers displaced in the lower part of flower, usually without pollen left, elongating style, no receptive stigma; stage V, young female stage, elongating style, stigmatic branches spreading out, start of stigma receptivity; stage VI, mature female phase, stigmatic branches totally spread out, maximum stigma receptivity; stage VII, advanced female stage, most stigmas receptive, flowers present signs of senescence like the curling of the inner lateral tepals. Broken lines in stages III, IV, and V indicate the position of the style.

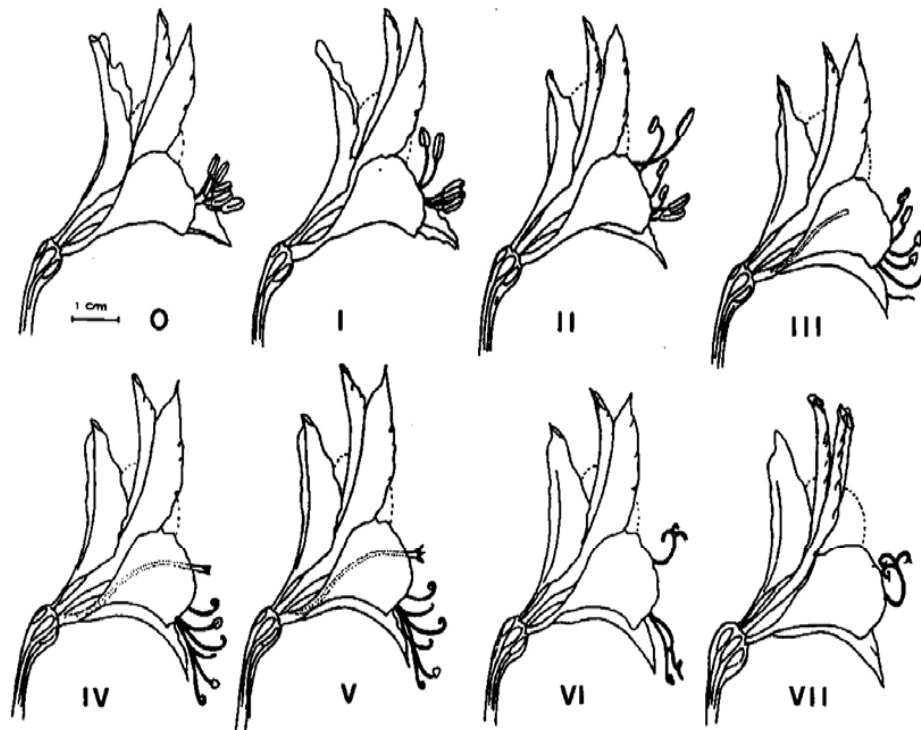
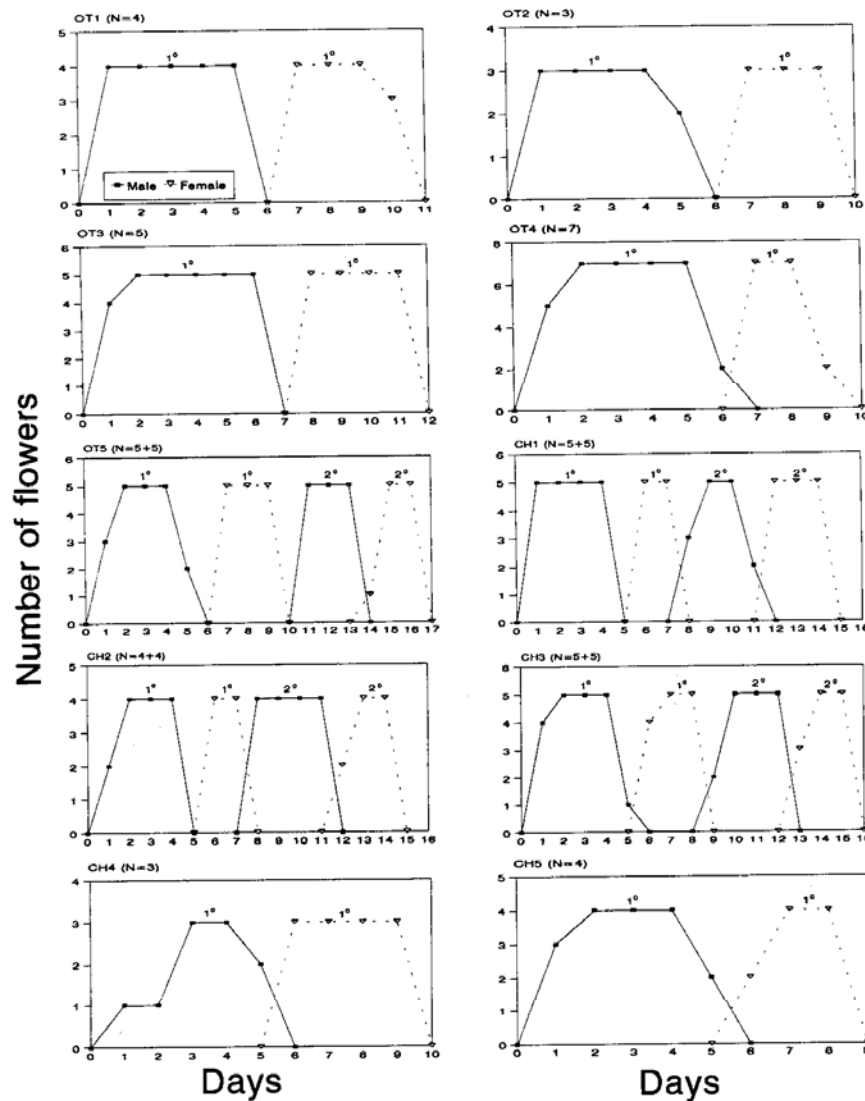




Fig. 3. The number of flowers in 10 haphazardly chosen ramets (5 from the Otto (OT) and 5 from the Challhuaco (CH) population) in male and female phases over time. Five ramets have simple and five have compound inflorescences. Day 1 is the day that the first flower of the ramet entered into the male phase. It is indicated whether each curve corresponds to the first ( $1^\circ$ ) or second ( $2^\circ$ ) whorl of flowers. The number of flowers of each ramet is also indicated (e.g.,  $N = 5 + 5$  means a ramet with 10 flowers total, 5 primary and 5 secondary).



Aizen, M.A. y A.  
Basilio. 1995. Within  
and among flower sex-  
phase distribution in  
Alstroemeria aurea  
(Alstroemeriaceae).  
Canadian Journal of  
Botany 73: 1986-1994.

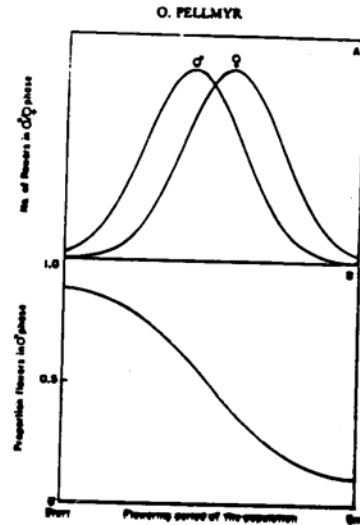


Figure 2. A, Proportion of flowers in male and female phases as a function of time in the flowering period in a theoretical population of a purely hermaphroditic, dichogamous species. Curves were drawn with effect as recorded for *Cimicifuga simplex* (20-day flowering period, 5-day effect). B, Proportion of hermaphrodite flowers in the male phase as a function of time in the flowering period, calculated from the curves in A. In both A and B, each flower has only been included the first day of each phase, since complete pollen removal and pollination typically occurred on that day. At lower pollinator density (where pollen remains in anthers and some stigmas remain unpollinated for a longer period), the slope of the functional sex ratio will be shallower and approaching 1:1.

#### EVOLUTION OF MULTIPLE SEX EXPRESSION

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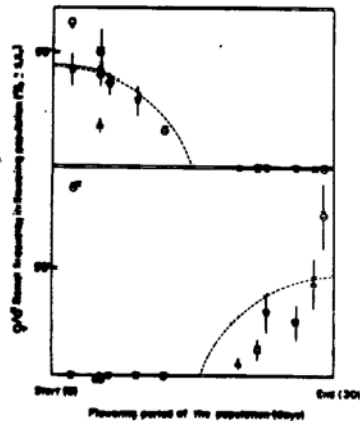


Figure 1. Proportion of unisexual flowers in five populations (different signs) of *Cimicifuga simplex* throughout the flowering period of each population. Curved lines denote percentage of unisexual flowers needed to balance the functional sex ratio of a pure hermaphroditic population with degree of dichogamy and flowering period as recorded for *C. simplex*. Sample sizes (in temporal sequence for each population) were: 25, 25, 40, 20; 25, 25, 55; 100, 115, 16; 100, 22; 160, 86, 20.

Pellmyr, O. 1987.  
Multiple sex expression  
in *Cimicifuga simplex*:  
dichogamy destabilizes  
hermaphroditism. Biol.  
J. Linn. Soc. 31: 161-  
174.

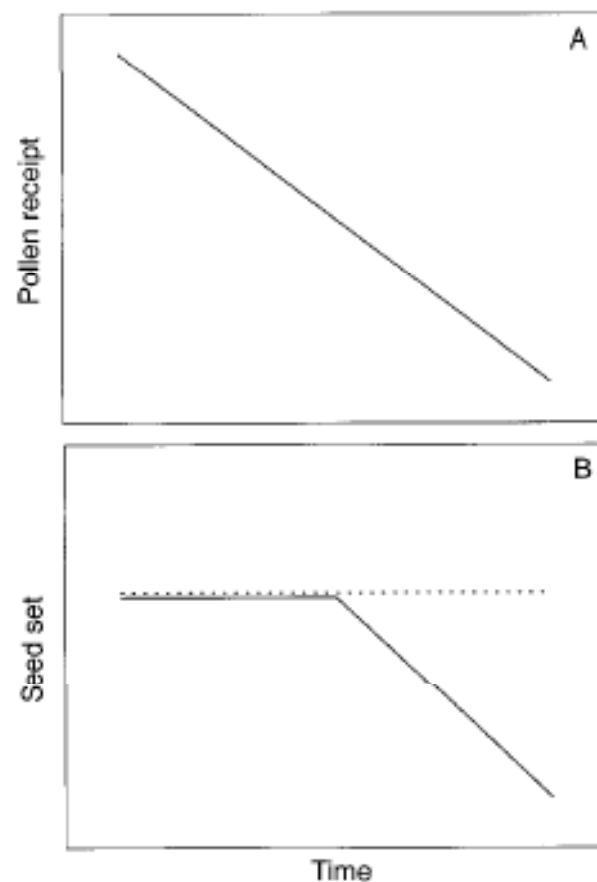


FIG. 1. Qualitative expectations of seasonal changes in (A) per-flower pollen receipt and (B) seed output under the scenario of a seasonal decrease in the proportion of male-phase flowers (= male sex ratio) over flowering phenology in *Alstroemeria aurea* in the upper Challhuaco Valley, Argentina. In (B), the solid curve depicts seed output expected under natural pollination conditions, and the dashed curve depicts seed output expected when flowers' stigmas receive excess pollen.

Aizen, M.A. 2001. Flower sex ratio, pollinator abundance, and the seasonal pollination dynamics of a protandrous plant. *Ecology* 82: 127-144.

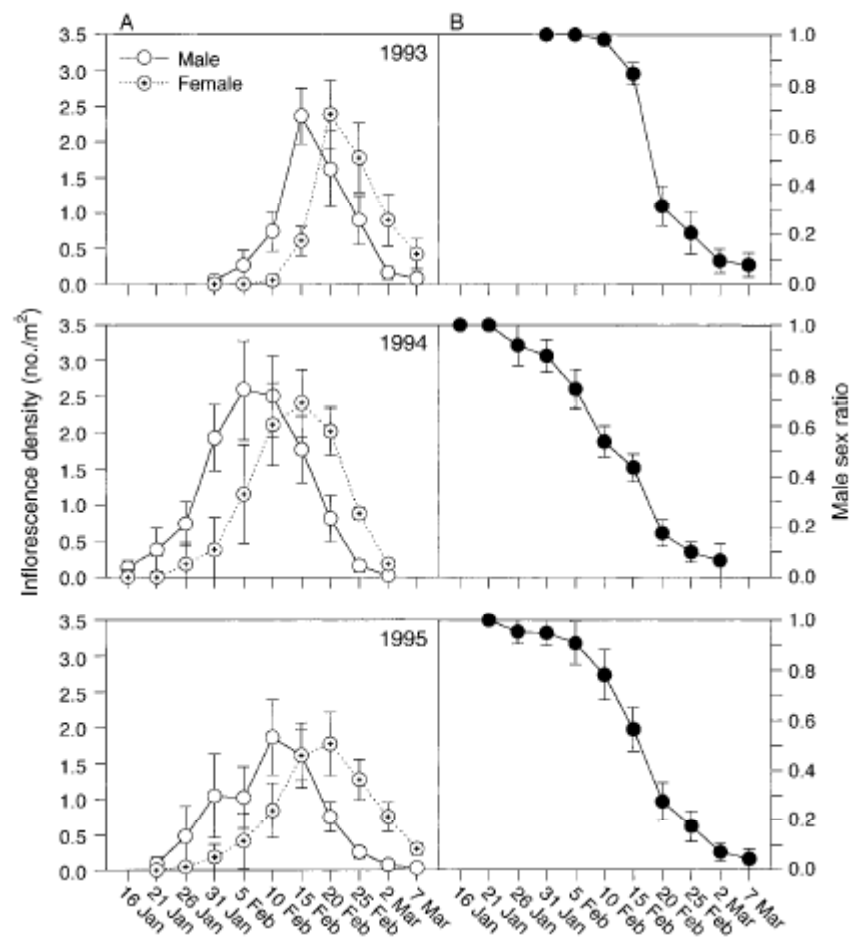


FIG. 2. Seasonal changes in (A) density of male and female inflorescences and (B) male sex ratio over the 1993–1995 flowering seasons. Values are means  $\pm$  1 SE;  $n$  = 14 plots.

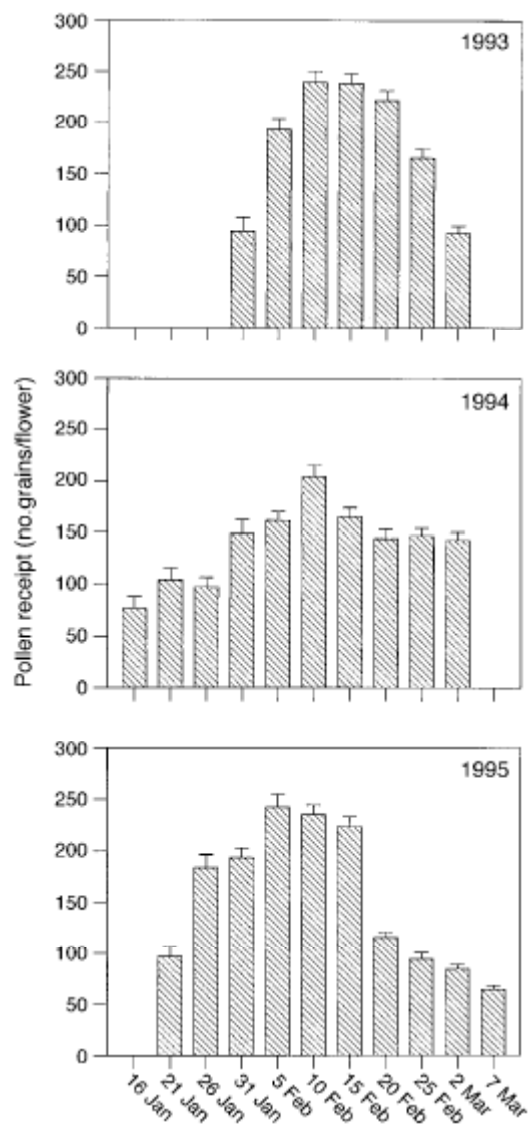


FIG. 3. Seasonal changes in total pollen receipt per flower over the 1993–1995 flowering seasons. Values are means  $\pm$  1 SE plotted against date.  $F$  values associated with one-way ANOVA were:  $F_{8,128} = 16.89$  (1993),  $F_{9,156} = 6.04$  (1994),  $F_{9,189} = 26.81$  (1995). In all instances,  $P < 0.0001$ . For each sampling date,  $n = 15$ –20 ramets.

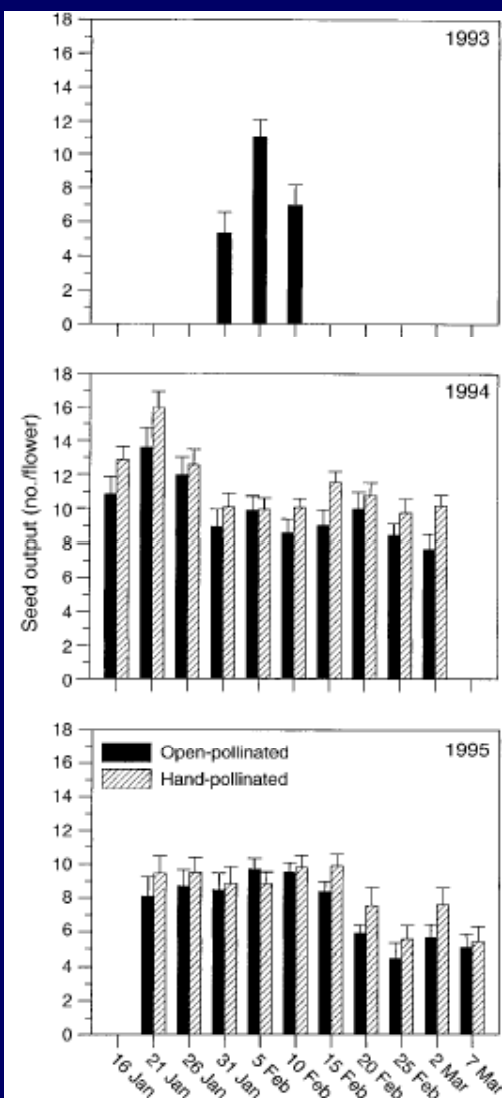


FIG. 4. Seasonal changes in seed output in open- and hand-pollinated flowers throughout the 1993–1995 flowering seasons. Values are means  $\pm$  1 SE plotted over date of the flowering season. In 1993, fruits developing from flowers that opened after 10 February could not be harvested because heavy snow buried them before maturation. For each combination of sampling date and pollination treatment,  $n = 15$ –20 ramets.

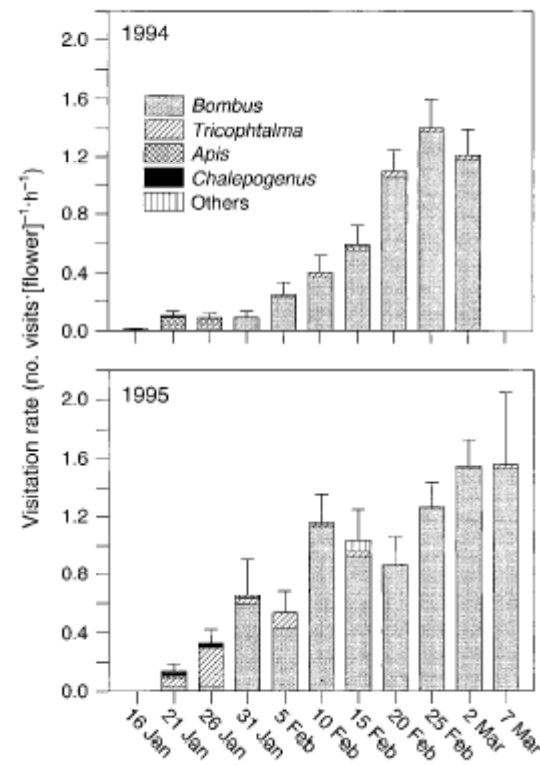


FIG. 6. Seasonal changes in visitation rates over the 1994 and 1995 flowering seasons (means  $\pm$  1 se). Values are mean visitation rates for each pollinator taxon plotted against the median date of 5-d time intervals. For the sake of clarity, only standard errors corresponding to mean visitation rates by all insects are depicted. Observations totaled 29 and 26 h over the 1994 and 1995 flowering seasons, respectively.



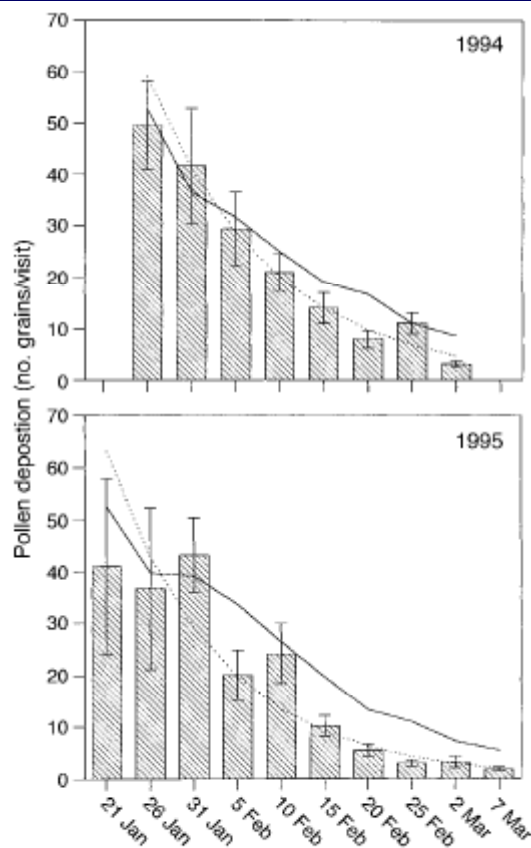


FIG. 8. Seasonal changes in per-visit pollen deposition on the stigmas of virgin female-phase flowers by bumble bee workers over the 1994 and 1995 flowering seasons. Values are means  $\pm$  1 se over the median date of successive 5-d periods. Dashed curves are the best-fitted regression equations  $\ln(\bar{y}) = 59.1 - 0.073x$  ( $r^2 = 0.920$ ,  $n = 8$ ,  $P < 0.0005$ ) for 1994 and  $\ln(\bar{y}) = 63.1 - 0.077x$  ( $r^2 = 0.932$ ,  $n = 10$ ,  $P < 0.0001$ ) for 1995. Back-transformed fits are depicted. Day 0 = 26 January 1994 and 21 January 1995, respectively. Solid lines pass through the values predicted by an empirical model of pollination efficiency based on the study of the effect of flower sex ratio on the process of pollen transfer (see *Materials and methods*). Total  $n = 318$  and 324 flowers for 1994 and 1995, respectively.

## A) Protandria y longevidad floral

	Protándrica	No protándrica	Total
<b>0-1 d</b>	117 (46.4%)	135 (53.6%)	252
<b>&gt; 1d</b>	52 (71.2%)	21 (28.8%)	73

$$G_1 = 7.42, P < 0.01$$

## B) Protandria y tipo de polinizador

	Protándrica	No protándrica	Total
<b>Abejas</b>	301 (59.4%)	207 (40.7%)	508
<b>Colibríes</b>	44 (32.8%)	90 (67.2 %)	134

$$G_1 = 30.02, P < 0.001$$

**TABLE 1. Incidence of monoecy and dichogamy in self-incompatible (SI) and self-compatible (SC) taxa<sup>a</sup>**

System	Percent incidence of system in self-fertility classes <sup>b</sup>		FAM <sup>c</sup>
	SI	SC	
Monoecy <sup>d</sup>	9.2 (130)	10.0 (250)	101
Intrafloral dichogamy <sup>e</sup>	71.2 (216)	71.3 (523)	103
Interfloral dichogamy <sup>f</sup>	95.7 (23)	95.3 (43)	25

<sup>a</sup> The original data set was truncated to reduce taxonomic redundancy as described in text.

<sup>b</sup> Numbers in parentheses are sample sizes.

<sup>c</sup> FAM is the number of angiosperm families included in the sample.

<sup>d</sup> Sexual system and self-fertility are independent in a contingency table ( $G = 0.03$ ,  $P > 0.05$ ).

<sup>e</sup> Intrafloral dichogamy and self-fertility are independent in a contingency table ( $G = 0.01$ ,  $P > 0.05$ ).

<sup>f</sup> Interfloral dichogamy and self-fertility are independent according to Fisher's Exact Test ( $P > 0.05$ ).

Bertin. 1993. Incidence of monoecy and dichogamy in relation to self-fertilization in angiosperms. *American Journal of Botany* 80: 557-560.

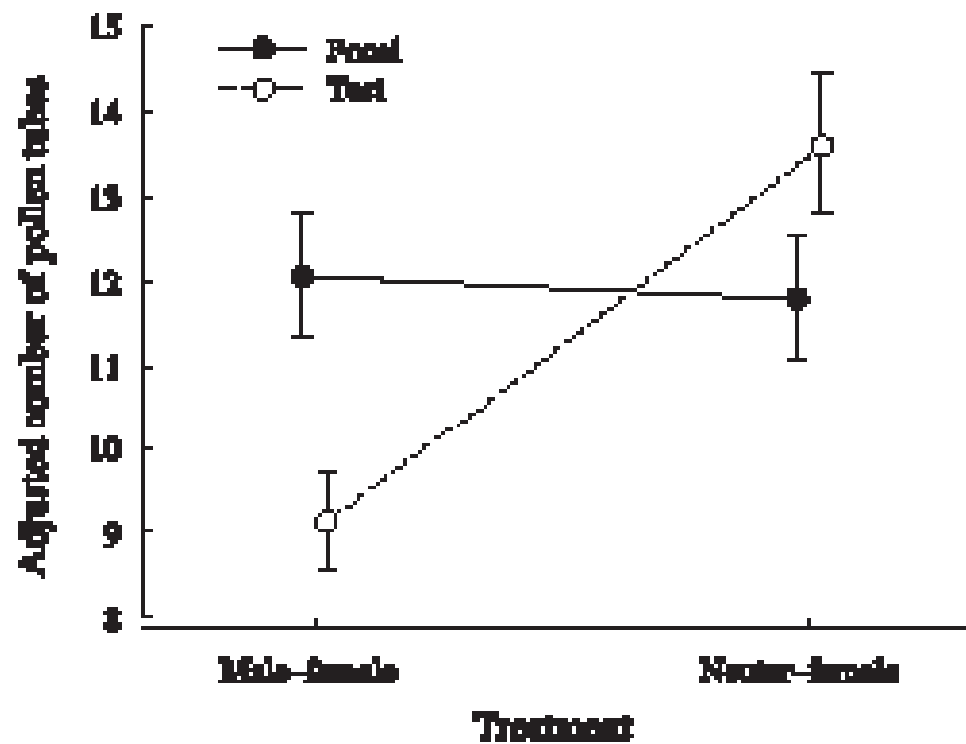


Fig. 5. Least-squares mean ( $\pm$  SE) number of pollen tubes in styles of male-female and neuter-female test and focal inflorescences after adjustment for variation in number of pollen grains on stigma.

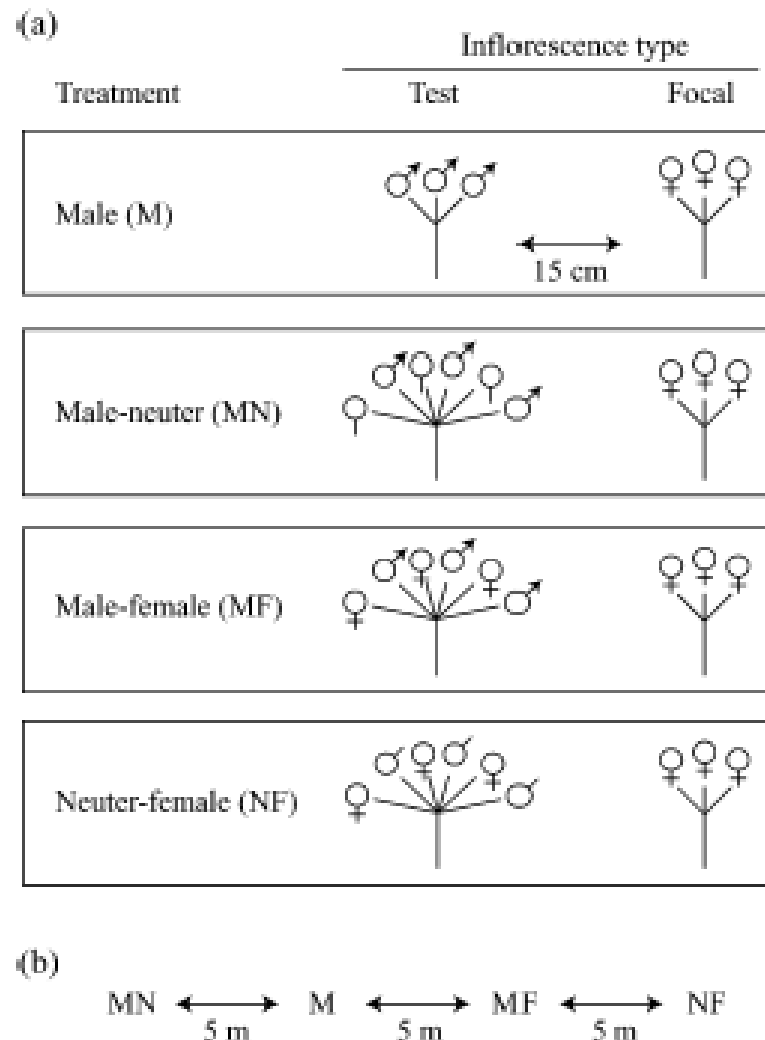
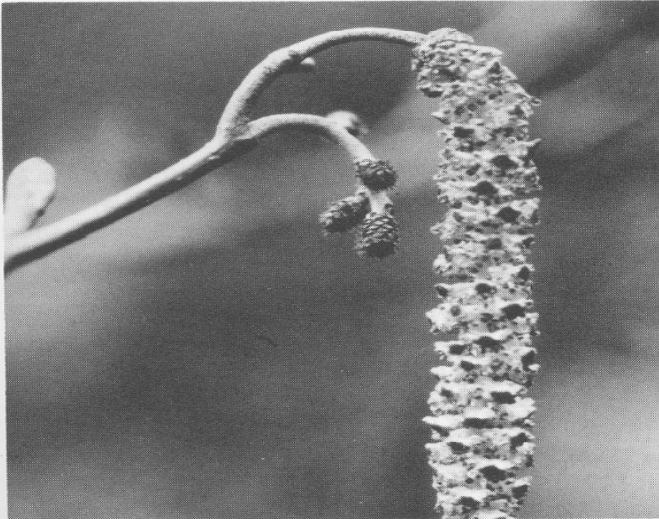


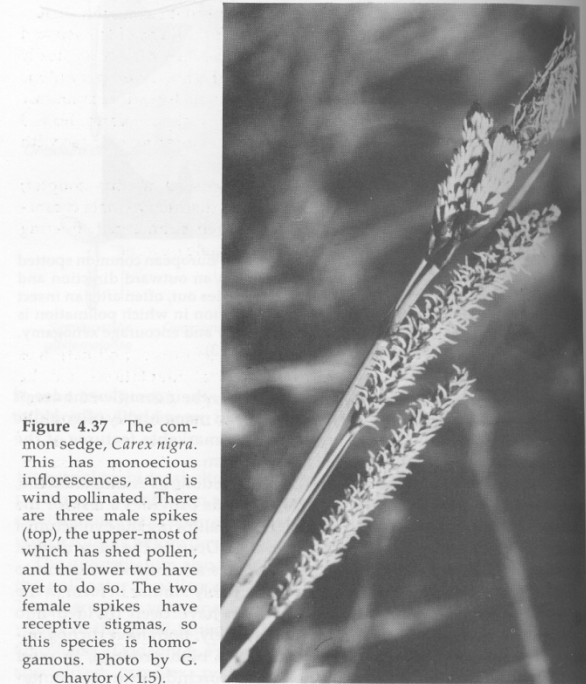
Fig. 1. Layout of the experimental design showing (a) characteristics of paired inflorescences in M, MN, MF and NF treatments; (b) example of spatial arrangement of the four treatments in a plot. Symbols: ♀ female flowers, neutered flowers without +, ♂ male flowers, neutered flowers without arrow.

Harder, L. y M.A. Aizen. 2004.  
The functional significance of  
synchronous protandry in  
Alstroemeria aurea. *Functional  
Ecology* 18: 467-474.

# Monoicismo



**Figure 1.2**  
The monoecious inflorescences of the wind-pollinated alder *Alnus glutinosa*. Female flowers on left, male flowers on right ( $\times 1$ ).



**Figure 4.37** The common sedge, *Carex nigra*. This has monoecious inflorescences, and is wind pollinated. There are three male spikes (top), the upper-most of which has shed pollen, and the lower two have yet to do so. The two female spikes have receptive stigmas, so this species is homogamous. Photo by G. Chaytor ( $\times 1.5$ ).



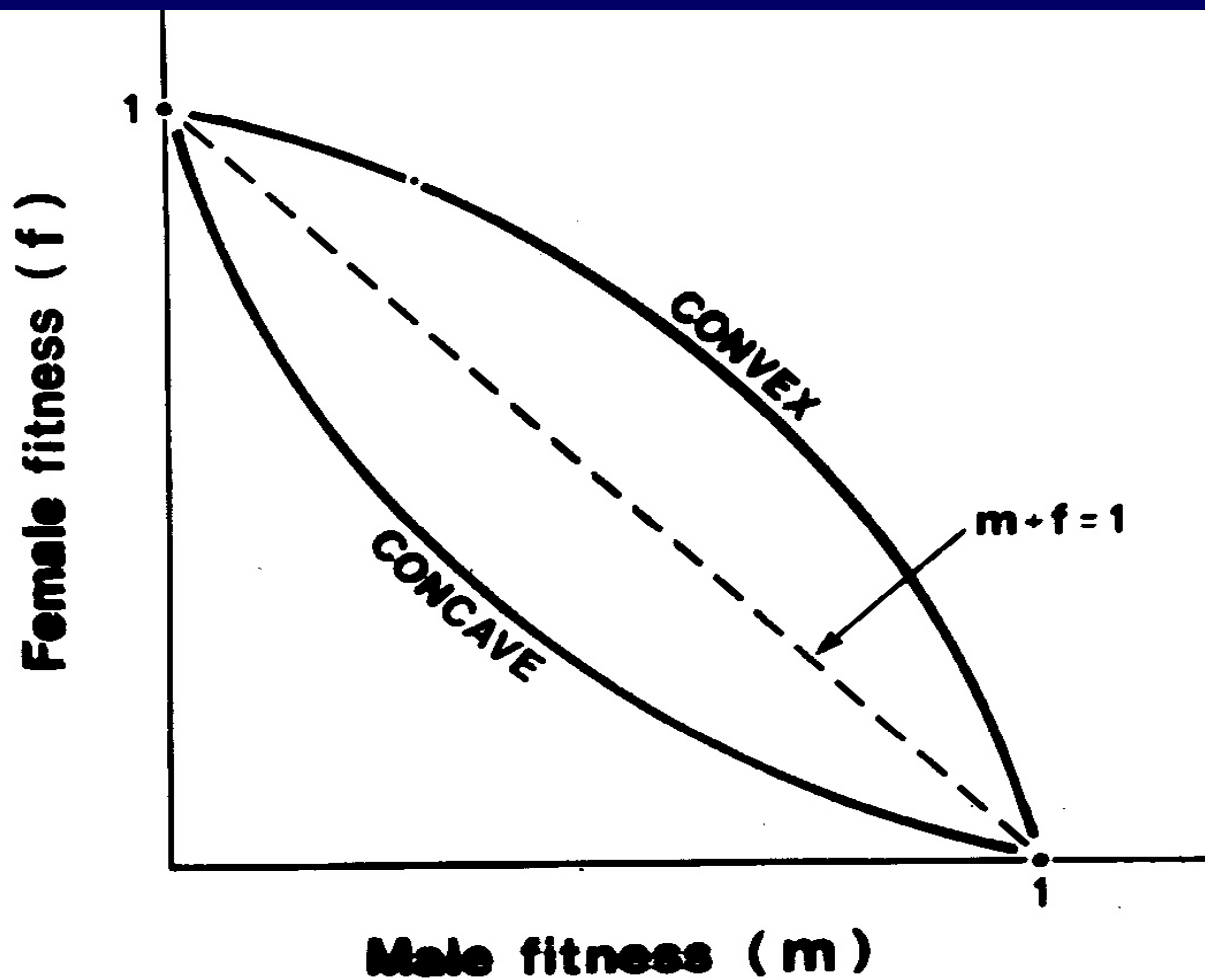


FIGURE 14.1. Possible fitness sets (*convex*, *concave*) for the tradeoff between male and female reproduction in a simultaneous hermaphrodite. Here, pure males and females (end points of the fitness set) have a relative fitness of one.

Charnov, et al. 1982. The theory of sex allocation. Monographs in Population Biology. Princeton University Press.

**Table 1.** Vegetative growth, fruit weight and date of female anthesis of functionally cosexual, male, female and neuter cucumbers

Functional gender	Growth measured in		Mean weight of fruit (g)	Mean date of F anthesis
	g dry wt	nodes		
M + F	18.06 (3.3)	24.85 (3.48)	12.95 (3.1)	23.90 (7.2)
M	39.01 (4.2)	33.89 (2.35)	—	—
F	19.85 (4.6)	24.65 (3.5)	12.34 (3.4)	23.10 (5.2)
O	40.70 (5.2)	35.33 (2.7)	—	—

Values are means of 20 (M + F & M) or 18 (F & O) replicates per treatment with standard deviations shown in parenthesis

**Table 2.** Analysis of variance of plant size at the end of the experiment based upon (a) plant dry weight and (b) number of nodes

(a) Source	Sum-of-squares	df	F-ratio	P
Male	7.336	1	0.78	0.380
Female	1842.471	1	195.99	<0.001
Male*	12.809	1	1.36	0.247
Female				
Error	676.879	72		
(b) Source	Sum-of-squares	df	F-ratio	P
Male	57.164	1	3.02	0.086
Female	8278.820	1	437.899	<0.001
Male*	0.044	1	0.002	0.962
Female				
Error	1361.215	72		

Silvertown. 1987. The evolution of hermaphroditism: an experimental test of the resource model. *Oecologia* 72: 157-159.

# Andromonoicismo



## Dioicismo

Alta incidencia en leñosas de bosques tropicales  
(20%, en herbáceas 5%)

Alta incidencia en flores de islas  
(13% NZ y 28% Hawaii vs. < 3% en floras continentales)

## Asociaciones con frutos carnosos:

Gimnospermas		
	Diocas	No diocas
Frutos carnosos	28	2
Frutos leñosos	2	38

## Asociaciones con frutos carnosos:

Angiospermas		
	Diocas	No diocas
Frutos carnosos	16	55
Frutos leñosos	3	282

Otros: Asociación con árboles que producen muchas flores y son polinizadas por insectos inespecíficos.



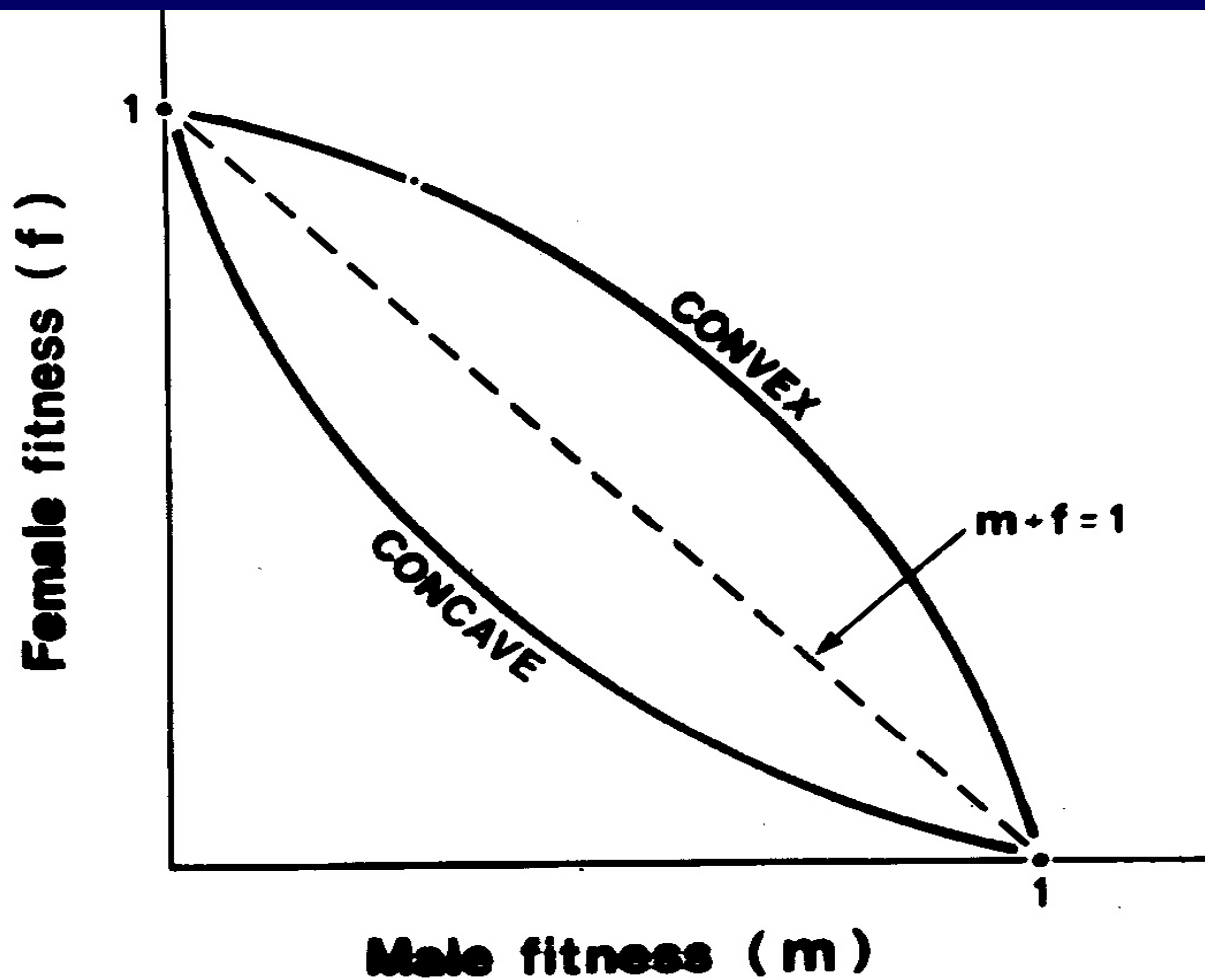


FIGURE 14.1. Possible fitness sets (*convex*, *concave*) for the tradeoff between male and female reproduction in a simultaneous hermaphrodite. Here, pure males and females (end points of the fitness set) have a relative fitness of one.

Charnov, et al. 1982. The theory of sex allocation. Monographs in Population Biology. Princeton University Press.

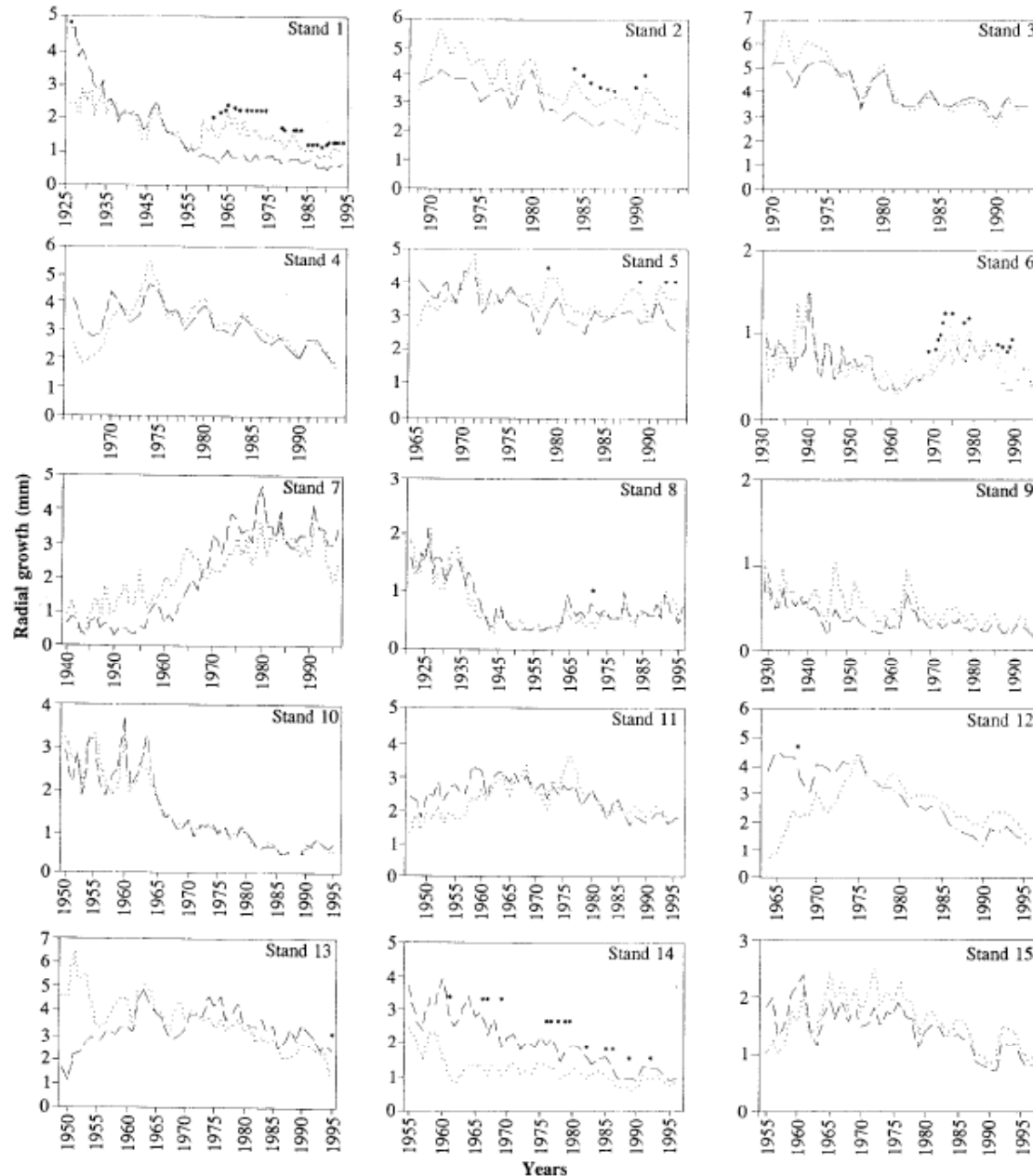
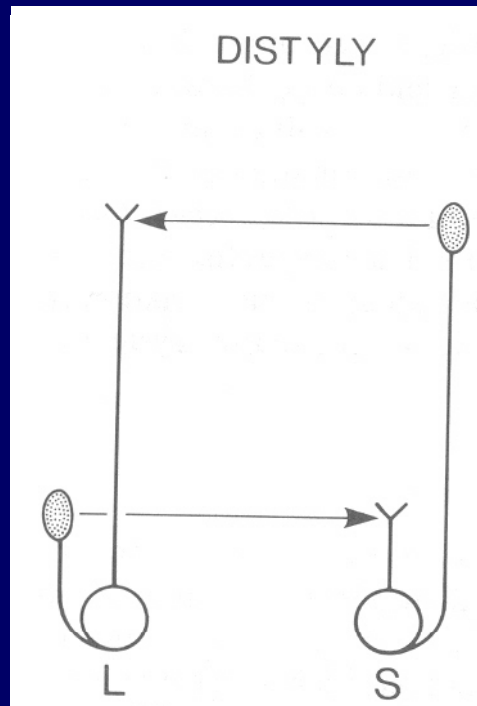


FIGURE 2. Radial growth of male (dotted line) and female (dashed line) trees. Asterisks indicate individual years in which significant growth differences between male and female were detected.

Rovere, A., M.A. Aizen y T. Kitzberger. 2003. Growth and climatic response of male and female trees of *Austrocedrus chilensis*, a dioecious conifer from the Temperate Forests of southern South America. *Ecoscience* 10: 195-203.

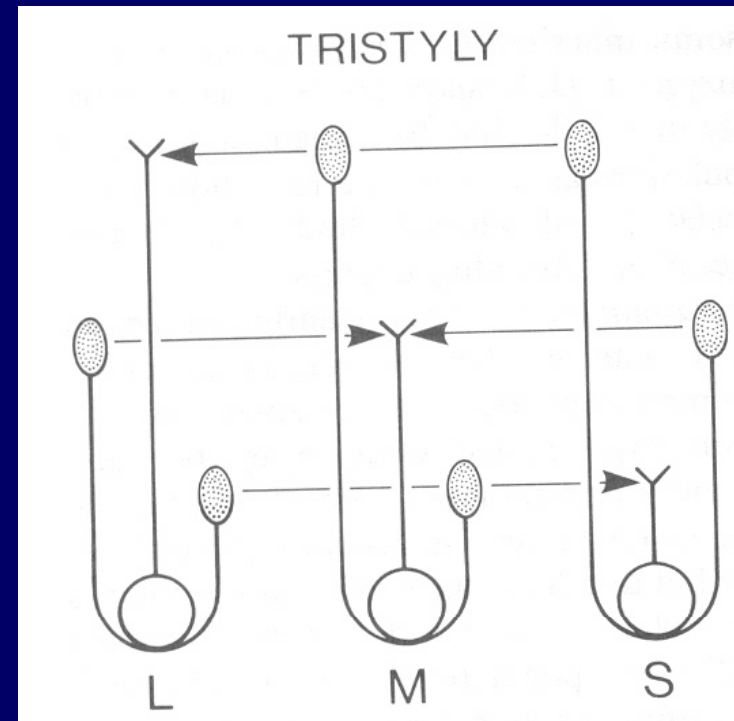
## Distilia



**ss**

**Ss**

*Primula*



**ssmm**

**ssM-**

**Ss--**

*Lythrum*

## Ginodioicismo

$$p = \frac{(f + 2sd - 2)}{2(f + sd - 1)}$$

$p$  es la proporción de individuos femeninos en el equilibrio.

$f$  es el fitness femenino comparado con el hermafrodita.

$s$  es el grado de selfing.

$d$  es la depresión por endogamia expresado como  $1-H/F$ .

# DICLINY

**Table 8.7** Reproductive performance of females in gynodioecious species expressed as a ratio to hermaphrodites (based on Godley 1979 and Stevens 1985)

Species		Flowers/ plant	Ovules/ flower	Seed/ ovule	Seed/ fruit	Seed/ plant	Weight
<i>Thymus vulgaris</i> (Assouad <i>et al.</i> 1978)		1	1	2.24– 3.25†	2.24– 3.25*†	3.14	
<i>Plantago lanceolata</i> (Van Damme 1984a)	MS1	1.69*	1	1†	1	1.69†	1
	MS2	1.69*	1	0.70†	0.70*	1.18†	
<i>Stellaria longipes</i> (Phillip 1980)		1.90†	1	0.92†	0.84	(1.60)	
<i>Geranium sylvaticum</i> (Vaarama & Jekelinen 1967)		0.69	–	–	1	(0.67)	
<i>Hirschfeldia incana</i> (Horovitz & Beiles 1980)		–	1.08	1.03†	1.11	–	1
<i>Leucopogon melaleuroides</i> (McCusker 1962)		–	1	1	1	–	
<i>Origanum vulgare</i> (Lewis & Crowe 1956)		–	1	1.19†	1.19*	–	
<i>Iris douglasiana</i> (Uno 1982)		–	1	1†	1	–	
<i>Saxifraga granulata</i> (Stevens 1985)		1	1	0.57*	0.58*	0.54†	

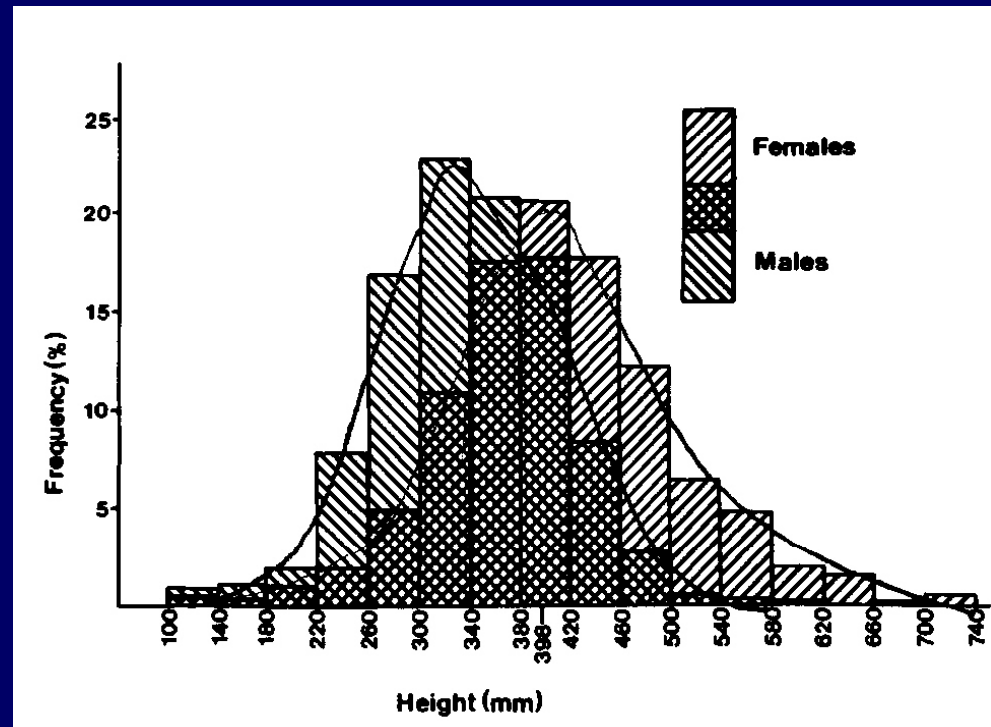
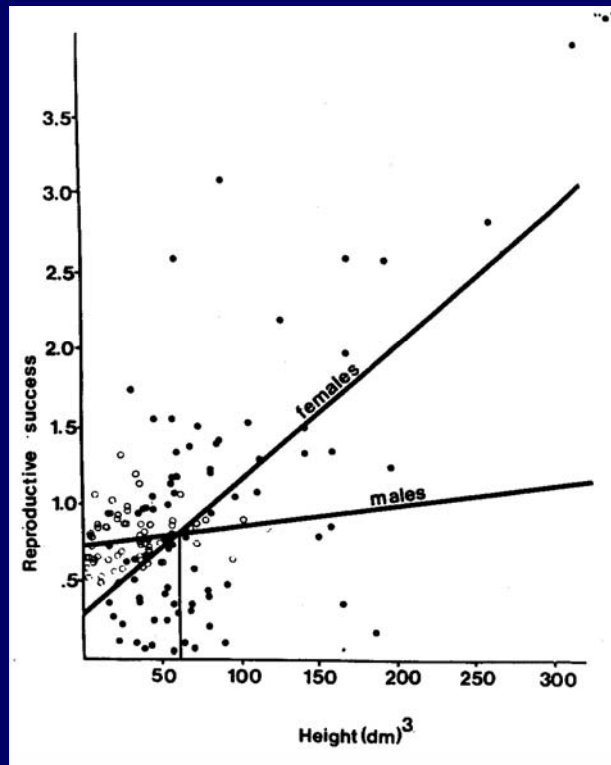
\* Stated to be significant at  $p < 0.05$  (results stated to be insignificant recorded otherwise reported as given by the authors).

† From cultivated plants.

‡ Calculated directly from other values in this table.

– No data.

## Disfasia sexual (plantas que cambian sexo)



Policansky, D. 1987. Sex choice and reproductive costs in Jack-in-the-pulpit. *BioScience* 37: 476-481.